

POLYDORA IN OYSTERS SUSPENDED IN THE WATER

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INTRODUCTION

Among the numerous enemies of oysters the small Polychaete worms of the genus *Polydora* have long been considered as very destructive. It has been reported that sometimes these worms may be responsible for the complete disappearance of extensive oyster beds. Such depredations were described by Whitelegge (1890) and Roughley (1922, 1925) who were working in Australian waters, where *Polydora* caused a heavy mortality among the native oysters. Both authors identified the worm as *P. ciliata*. It is possible, however, that Whitelegge was mistaken in his identification of the species. According to Wilson (1928) "Whitelegge found the ova and larvae of a species of *Polydora* attached alongside the adults to the walls of their burrows in oyster shells at Newcastle, in New South Wales. He believed the species to be *Polydora ciliata* Johns, but his figure of the egg-sacs resembles more closely that given by Söderström for *Polydora ligni* Webster." If Whitelegge was actually mistaken then the destruction of the oysters in Australian waters should be attributed to at least two species of *Polydora*, namely, *P. ciliata* and *P. ligni*.

Several species of *Polydora* are common along our Atlantic Coast. Lunz (1940, 1941) found that approximately 40 per cent of the oysters of South Carolina waters are infested with *P. ciliata*. This author states in his latest paper that he now has evidence or reports of infestation throughout the entire range of distribution of the American oyster, *O. virginica*, in North America. Nelson and Stauber (1940) stated in a brief abstract that many oysters of New Jersey harbored *P. ligni* Webster. This appears to be the same species which, in the opinion of Wilson, Whitelegge was dealing with in Australia. Kavanagh (1940) found that the Japanese oyster, *O. gigas*, planted in Louisiana waters became infested with *P. ciliata*. Takahashi (1937) reported that *P. pacifica* was quite commonly present in the shells of the pearl oyster, *Pinctada margaritifera*.

Polydora or, as it is usually called, mud worm, is also known to infest shells of mollusks other than oysters. Lebour (1907) found that the mussels of the Northumberland beds of England were heavily infested with *P. ciliata*, and Field (1922) stated that the same species occurs in shells of the mussel, *M. edulis*, living in American waters.

Polydora usually gains entrance into the oyster while the worm is still in the larval stage, or when very young (Wilson, 1928; Roughley, 1925). Soon after entering the oyster the worm builds two mud tubes at right angles to the edge of the shell. The accumulated mud irritates the oyster tissue and the mollusk, in self protection, secretes a layer of shell material over the mud tubes. A description of the formation of mud blisters has already been given by Whitelegge (1890) and Lunz (1941) and need not be repeated here.

It has been the opinion of many investigators that the oysters infested with *Polydora* are usually very poor. If the infestation persists, they gradually begin to weaken and eventually succumb (Roughley, 1922; 1925). In some instances, as for example in Australia, it has been considered advisable to grow these mollusks on stones, logs or on specially constructed platforms, away from the bottom. Roughley (1922, 1925) believes that the method of keeping the oysters above the bottom mud is an effective means of preventing the infestation. It appears that Roughley's observations and data fully justify his conclusions in regard to the conditions existing in Australian waters. However, recent work of the authors carried on in Milford Harbor on the Connecticut side of Long Island Sound, showed that some of the habits of our species of *Polydora* and its effects on American oysters are somewhat different from those described for the Australian species, or previously ascribed to the mud worms common in American waters.

Description of P. Websteri Hartman

The mud worm found in the oysters of Milford Harbor was identified by Dr. Olga Hartman of Allan Hancock Foundation, The University of Southern California, as *Polydora websteri* Hartman, new name. In personal correspondence with the authors Dr. Hartman states that the original description of the worm, as *P. caeca*, was published by Webster, 1879. Since the description is faulty and misleading in all essential respects, it has little value for systematists. Dr. Hartman expresses an opinion that, unless caution is taken, the next reviser or systematist is almost certain to refer to our species as the European *P. ciliata*, since its morphological characters are closely akin to those of the latter. To avoid constant confusion of *Polydora websteri*, which at present is a systematically unknown species, with *P. ciliata* and some other species of *Polydora* that are known to be very numerous in eastern America, Dr. Hartman suggested that a description and the illustrations clearly indicating the characters of the worm should be given in this article. In accordance with the suggestion a description of *P. websteri* and the illustrations showing some of its morphological characters are offered here. Both the description and illustrations were prepared by Dr. Hartman.

“*Polydora websteri* Hartman

Polydora caeca Webster, 1879, Trans. Albany Inst., vol. 9, pp. 252-253, Figures 119-122 (not Oersted, 1843).

Polydora websteri Hartman (1942 MS on Beaufort Annelids).

The total length consists of about 105 segments and measures (preserved) 20 mm. long or shorter, but the body is usually much contracted and coiled up. The prostomium is clearly bifid at its anterior margin; it may lack eyes or there may be 3 or 4 weakly developed ones in trapezoidal arrangement; the prostomial parts, palpi omitted, are shown in dorsal (Figure 1, a) and ventral (Fig. 1, b) views. The first segment has a notopodial lobe but no notosetae, and the neuropodium is provided with a fascicle of slender setae. The second to fourth segments are biramous and have larger fascicles of notosetae and neurosetae with posterior lamellae. The fifth or modified segment is longer than the others and has, on either side, a dorsal fascicle of heavy yellow hooks with companion

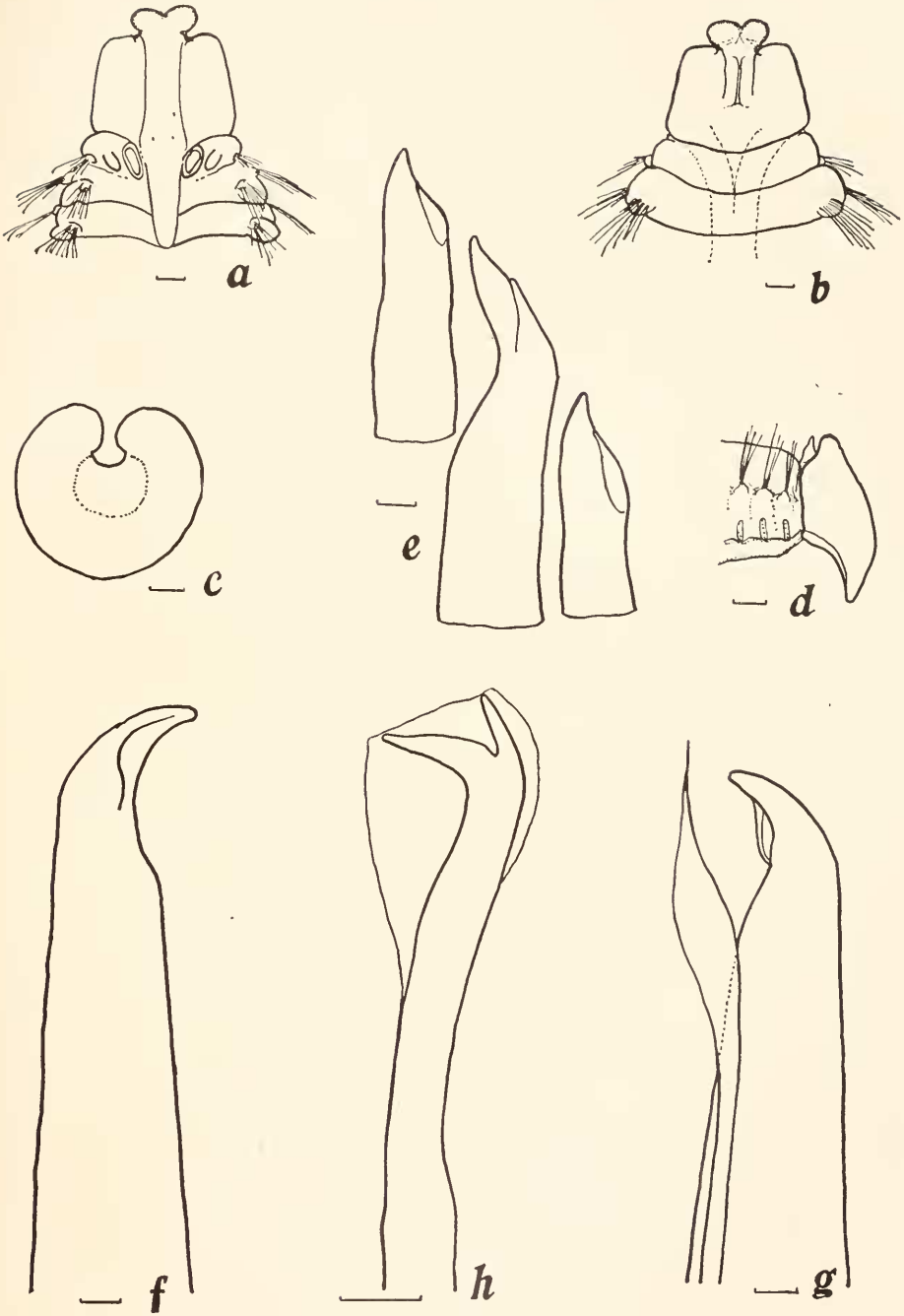


FIGURE 1. Showing certain morphological characters of *P. websteri*. Explanation in the text.
 (Courtesy of Dr. Olga Hartman.)

pennoned setae, and a ventral fascicle of 5 or 6 pointed setae. The seventh setiger has pointed setae in both fascicles. Hooded hooks are present from the neuropodium of the eighth setiger and continued posteriorly to the end. There are no specialized hooks in the last segments. The posterior end terminates in a flattened collarlike disk with a dorsal notch (Fig. 1, c in posterior view) considerably wider than the last few segments (Fig. 1, d in lateral view).

Branchiae, first present from the seventh setiger, are at first small but gradually enlarge to their full size in about 5 segments; they are continued through most of the body length but gradually decrease in size in the posterior fourth and are absent from the last 15 or 16 segments.

The heavy hooks of the fifth setiger number about 6 projecting ones in a fascicle; they are unique in that the falcate distal end has a hard, chitinous sheath around one side; various views are shown for projecting (Figs. 1, f, g) and embedded (Fig. 1, e) ones. The companion pennoned setae (Fig. 1, g) when perfect terminate in an acute point but some may be broken off and appear frayed at the distal ends. The hooded hooks number about 6 in a series in the middle of the body; they have 2 well developed teeth, the major one at a right angle to the shaft (Fig. 1, h). Tubes are fragile, constructed of silt and debris incorporated with mucus, and occur in calcareous shells.

The original description as *P. caeca* Webster is incomplete in some important details and erroneous in some others. The first segment has neurosetae, not notosetae; the pygidium is interrupted above, not below; the companion setae of the modified segment are pennoned, not capillary; the modified hooks of this segment are not merely falcate but have a sheath that extends some distance around it. There may be weakly developed eyespots.

P. websteri resembles *P. ciliata* (Johnston) (Fauvel, 1927, Faune de France, Vol. 16, p. 49) in some respects but the two differ in that the first has a prostomial caruncle that extends posteriorly to the end of the third setiger and the modified spines of the fifth setiger have a sheath around one side; in the second the prostomial caruncle extends posteriorly to the second setiger and the modified spines have an acute tooth in the concave part of the spine.

The single individual on which Webster's description was based is not known to exist. The collection on which the present description is based is deposited in the Allan Hancock Foundation of the University of Southern California. It was collected from vesicles on empty oyster shells, in the mouth of the Milford River, by Mr. J. B. Engle of the Milford Wildlife Laboratory. Since 1937 I have obtained this species in considerable number from Beaufort, North Carolina, Lemon Bay in southwestern Florida, and Virginia north to Connecticut. It may be widely distributed in intertidal zones of temperate North America.

(On the plate, the small scale near the label indicates 1 mm. for prostomium and pygidium and 0.1 mm. for setal structures.)"

The authors wish to express their appreciation to Dr. Olga Hartman for the identification of our species of the mud worm and for preparation of the description and the illustrations of the morphological characters of *P. websteri*.

OBSERVATIONS

These studies were begun in April, 1940, when five large groups of oysters, ranging from one to 5 years of age, were placed under observation in Milford

Harbor. In the summer of the same year another group, composed of individuals of the 1940 set, and thus being only a few weeks old, was added. Altogether over 1000 animals were used in the experiment. All these oysters were brought from the deep water beds of Long Island Sound, where *Polydora* is very uncommon. Examination of the oysters showed that only about 2 per cent of them had mud vesicles.

Oysters of each year-class were placed on separate, large, wire trays, suspended in the water from a float, which rose and fell with the tide. Even at low tide the trays were at least four feet above the bottom. The oysters remained suspended in the water until November 1, 1942. Thus, the experiment lasted $2\frac{1}{2}$ years, and

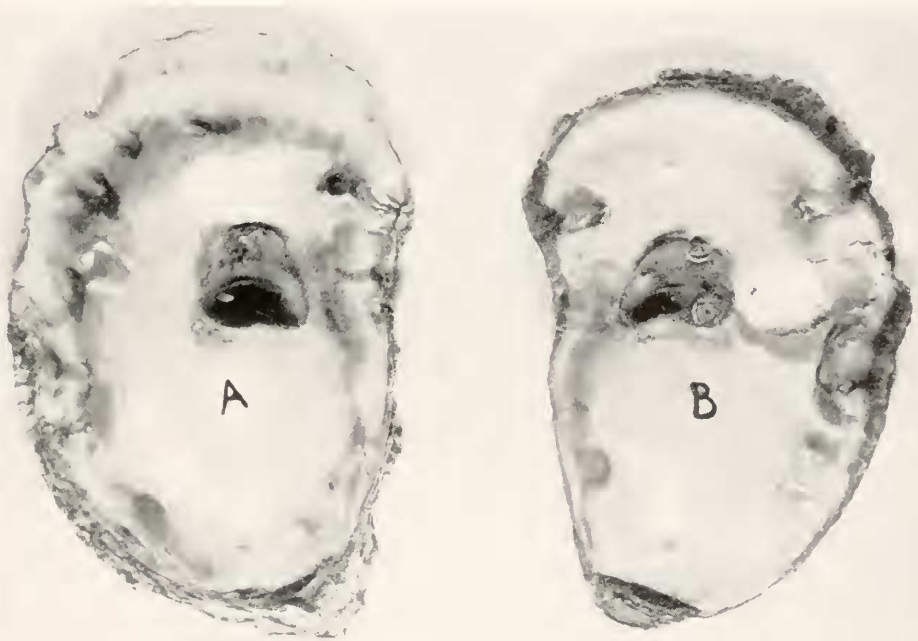


FIGURE 2. Shells of an oyster infested with *P. websteri*. A. Cup valve. B. Flat valve.

covered two winter and three summer periods. At the end of the experiment a random sample consisting of 20 oysters was taken for examination from each year-class group. All the oysters were opened and the condition of their shells and meats noted.

Examination of the shells showed that the oysters of all year-classes were heavily infested with *Polydora websteri* (Fig. 2). This was true even for those of the 1940 class which were but several weeks old when placed on the trays. The infestation was so heavy that in many instances separate mud vesicles could not be distinguished. Usually the combination of several vesicles formed large mud blisters. All the shells, with exception of one flat valve belonging to an oyster of the 1940 class, were infested. The class of 1935, comprised of the oldest oysters, had the greatest number of vesicles and blisters, while the youngest class had the

least (Table I). However, since the shells of the older oysters offered much larger areas for infestation than those of the younger class, no direct relationship between the age of the animals and the degree of infestation could be assumed. Such a conception was further sustained by the lack of correlation between the age of the oysters and the degree of infestation in the other four year-classes (Table I). In general, the cup valves of the oysters contained more vesicles and blisters than the flat valves. This again cannot be regarded as significant because the surface of a cup valve is considerably larger in area than that of a flat one.

Careful examination of the character and positions of the mud vesicles, and the location of the characteristic double holes on the exterior of the shells through

TABLE I

Number of mud vesicles and blisters found in shells of oysters of different ages grown on the suspended trays and on the bottom. Each sample consisted of 20 oysters.

YEAR CLASS	TRAY OYSTERS				BOTTOM OYSTERS			
	Cup valve		Flat valve		Cup valve		Flat valve	
	vesicles	blisters	vesicles	blisters	vesicles	blisters	vesicles	blisters
1935	208	31	177	27	13	1	17	3
1936	136	3	103	2				
1937	188	20	123	17				
1938	208	39	111	24				
1939	189	33	156	28				
1940	126	20	81	8	3	0	4	0

which the worms communicate with the outside, as well as studies of the cross-sections of the shells clearly indicated that the infestation was not confined exclusively to any one year within the experimental period. It was found, as the result of such examination, that the infestation with *Polydora* began during the summer of 1940 and continued until the end of the experiment.

While examining the shells of the oysters it was noted that in many instances of severe infestation as many as six or seven layers of blisters, superimposing one over the other, could be found over the same shell area. The worms occupying the lowest, and therefore the oldest, blisters were of a larger size than those of the upper ones. The occupants of the upper blisters were, as a rule, very small, indicating that they entered the shell only a short time before examination. Even under such apparently overcrowded conditions the majority of the worms were alive and, judging by the quantities of accumulated mud, very active.

Discovering an unusually heavy infestation of the tray oysters, it was decided to compare the degree of infestation of these animals with that of the mollusks living on the muddy bottom. For this, samples of 20 oysters of the 1935 and 1940 year-classes were taken from the bottom of Milford Harbor, in the area where the float with the suspended oysters was stationed during the experiment. Examination of the shells of the bottom oysters revealed that they were much less infested than those kept suspended in the trays. Many bottom oysters of the two year-classes were entirely free of mud worms. In the 1935 class, nine

cup valves and seven flat ones bore no signs of infestation. The class of 1940 was in even better condition, because 17 cup and 16 flat valves were entirely free of vesicles or blisters (Table I).

In examining the condition of the oysters removed from the trays it was noted that, regardless of the very large number of mud worms infesting their shells, the oyster meats were in an excellent condition. They were unusually "fat," and large in size. They appeared much superior to those of the oysters usually grown in Milford Harbor. To verify this, a comparison was made of the experimental oysters and the animals taken from the bottom of Milford Harbor. It consisted in comparing the weight of the oyster meats in relation to their total weight. Each sample consisted of 20 oysters. The results obtained indicated that the animals suspended on the trays were much better than those collected from the bottom (Table II). This was especially true of the oysters of the 1935 year-class,

TABLE II

Average total weight and weight of meat, and per cent of meat of oysters of different ages grown on the suspended trays and on the bottom.

YEAR CLASS	TRAY OYSTERS			BOTTOM OYSTERS		
	Total weight	Weight of meat	Per cent of meat	Total weight	Weight of meat	Per cent of meat
1935	280.4	28.3	10.1	232.5	13.2	5.7
1936	216.2	22.1	10.2			
1937	202.0	21.9	10.8			
1938	154.2	17.2	11.1			
1939	122.1	15.0	12.3			
1940	73.1	10.1	13.7	21.8	2.4	11.0

where the bottom animals were found to be rather poor. The condition of the bottom oysters of this age-group was further substantiated by the observations made in connection with another series of experiments, dealing with seasonal changes in oysters in Milford Harbor. Samples of these oysters examined on November 15 and December 15, 1942, showed that on those dates the weight of their meats constituted 6.5 and 5.9 per cent of their total weight.

On the basis of the above described observations the conclusion may be formed that a heavy infestation with *P. websteri* does not necessarily render the oysters poor. As was mentioned previously, the meats of heavily infested tray oysters were in an unusually good condition. Such a condition, of course, cannot be ascribed to commensalism with *P. websteri*. It indicates, nevertheless, that a heavy infestation of their shells does not prevent oysters from becoming "fat," provided other environmental conditions are favorable for the existence of the mollusks.

Regardless of the fact that the experimental oysters were suspended on the trays, away from the bottom, they were, nevertheless, covered with a very heavy layer of the deposit consisting of silt, mud and various dead and alive plankton forms. The thickness of this layer usually varied between 1/8 and 1/4 of an inch. Such accumulation of muddy substance was more than sufficient to supply the worms with all the mud needed for their activities. Therefore, no question could

be raised whether or not there was enough mud to be carried by the worms for deposition between the shells of the oysters.

Indirectly, the experiments also provided an answer to the question of whether or not a severe infestation with *P. websteri* always causes a heavy mortality among the oysters affected. This answer is negative. For example, the most heavily infested year-class was that of 1935. In November 1941, this group consisted of 94 oysters. At the end of the experiment, in November 1942, 90 of these animals were still alive. Therefore, during the last year of the experiment, when infestation with the mud worms was presumably the heaviest, only four animals of the total number of 94 died. Thus, the mortality for the entire year amounted to only 4.3 per cent. This figure is considerably below that of the mortality of oysters of the same age but living under natural conditions, where a death-rate from 8 to 10 per cent is considered as normal.

It was also observed that a heavy infestation with mud worms did not interfere with the rapid growth of the oysters. All year-classes of suspended oysters, although heavily infested, showed a considerable increase in growth. The rate of growth greatly exceeded that of the less infested oysters living under natural conditions. The most noticeable difference was recorded in the case of the 1940 year-class, where at the end of two years, the average length of the suspended oysters was 79.2 mm. as compared with 63 mm. for the bottom oysters. Incidentally, our observations that the oysters kept off the bottom showed better growth are contradictory to those of Nelson (1921) who, on the basis of his experiments in which he also used wire trays, stated that "There was no appreciable difference in the rate of growth of oysters on the bottom from that of oysters on the platform above."

DISCUSSION AND SUMMARY

It has been generally assumed that several species of Polychaete worms, such as *P. ciliata* and *P. ligni*, are very dangerous enemies of oysters interfering with their fattening and growth, and often causing a heavy mortality among them. It has also been stated that a heavy infestation with *Polydora* can be avoided if the oysters are grown away from the bottom mud. The method of growing oysters off the bottom is widely used in Australia.

Results of the experiments conducted for a period of 2½ years in Milford Harbor, Connecticut, indicate that in this body of water certain aspects of the behavior of at least one species of *Polydora* and its effects upon infested oysters are different from those observed in Australian waters, or ascribed to the mud worms of certain sections of our Atlantic Coast.

The Milford experiments have shown that mud worms, *Polydora websteri*, were found in much larger numbers in the shells of the oysters suspended in the water for a period of 2½ years than in those living on the muddy bottom. This indicates that in some areas along the Atlantic Coast of North America the suspension of oysters away from the bottom does not prevent, or eliminate, their infestation with the mud worms, *P. websteri*. Results of the experiments also point to the conclusion that the method of suspension may be regarded as providing sometime more favorable conditions for the mud worms to infest the oysters.

A complete explanation as to why the mud worms preferred the tray oysters to those on the bottom is still lacking. It may be suggested at this time, never-

theless, that the difference in salinity at the bottom, and in the zone where the oysters were suspended might have played an important part in the degree of infestation of the two groups. In Milford Harbor, which is a body of water affected by the river discharge and by inflow of salt water from the Sound, the salinity of the upper layers of the water is usually lower than that observed near the bottom. At times such differences are of considerable magnitude. For example, during the rainy period of 1942 occurring in August, the salinity of the surface layer varied between one and five parts per thousand, whereas at the bottom the salinity remained quite steadily above 25 parts per thousand. The fact that the heavily infested tray oysters were living in less salty water than those existing on the bottom may indicate that *P. websteri* prefers the water of considerably reduced salinity. Lunz (1941), on the basis of his observations in South Carolina, is also of the opinion that *P. ciliata* is more prevalent in water of low salinity.

The suggestion that *P. websteri* does not readily infest the oysters living in water of comparatively high salinity is substantiated by the authors' examination of oysters collected from Long Island Sound proper. During the summer of 1942 several thousand oysters of all ages were opened and examined. They were collected from many sections of the oyster-producing area of Connecticut. Very few oysters were found infested with Polydora. The salinity of the water of the area from which the samples were collected is usually above 26 parts per thousand (Loosanoff and Engle, 1940).

If certain species of Polydora, such as *P. websteri*, prefer water of low salinity, it is quite possible that several outbreaks of infestation of oysters with mud worms may be the result of prolonged rainy periods. In such cases large quantities of fresh water entering inshore shallow areas may considerably reduce the salinity of the water in which oyster beds are located, thus providing favorable conditions for the spreading of Polydora infestation. Experiments on the effects of various salinities upon the activities of Polydora, which are now being conducted by the authors, may throw additional light upon this very interesting and important subject.

Regardless of the heavy infestation with mud worms the meats of the tray oysters were in a far better condition than those of the mollusks living on the bottom. Their growth was also more rapid than that of the less infested animals of the same ages, but living under natural conditions. These two observations indicate that a heavy infestation with *P. websteri* does not necessarily interfere with the feeding and fattening of oysters, nor impair their growth. The apparent lack of ill effects upon the growth and fattening of oysters can be easily understood, if it is remembered that Polydora is not a parasite. Each worm remains in contact with the fleshy tissues of the oysters for a comparatively brief period. As soon as the mollusk covers the intruder and its mud tubes with a layer of shell material, the worm becomes isolated and cannot exert toxic effects upon the tissues of the oyster. It is probable, nevertheless, as Lunz (1941) indicated, that a large number of mud blisters within the shell may restrict the living space of the oyster, and that the animal may be forced to spend considerable energy in secreting the shell material for covering the mud worms. It is also possible that large quantities of mud accumulated by the worms on the bottom may render

the environmental conditions unfavorable for the existence of the oysters and may even cause a heavy mortality among those mollusks (Roughley, 1922).

Milford experiments have also shown that a severe infestation with *P. websteri* did not cause a heavy mortality of the oysters. Our observations coincided with those of Lunz (1941) on *P. ciliata* who found that "In the five year period during which these pests have been under observation in South Carolina and other southern states, no high mortality has been found on oyster beds which could be attributed to the activities of Polydora."

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